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First report of moth pollination in *Struthiola ciliata* (Thymelaeaceae) in southern Africa

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Abstract

Struthiola ciliata (L.) Lam., an ericoid shrub widespread in fynbos vegetation in the southwestern Cape, displays the floral syndrome associated with pollination by settling moths. Flowers, which are produced throughout the year, are creamy white in colour, with a slender hypanthium tube ±20 mm long. The anthers are included within the tube and the mouth of the tube is surrounded by eight fleshy petaloid scales. Anthesis takes place in the evening at ±18h00, at which time the flowers begin to emit a strong, sweet, spicy and somewhat coniferous fragrance from the petaloid scales. The compounds thujone, isothujone, verbenone, α-terpineol, benzyl acetate, eugenol and vanilline are the main components of the scent profile detectable by the human nose. The cells of the petaloid scales are densely cytoplasmic and contain numerous oil droplets. Starch-rich tissue is located near the mouth of the hypanthium tube. Flowers accumulate small volumes (0.025–0.188 μl) of moderately concentrated nectar (20–34% sucrose equivalents) in the hypanthium tube. Individual flowers last for 9 to 11 days, with nectar secretion restricted to the first 3 to 4 days. The only floral visitors observed were the moths *Syngrapha circumflexa* (Linnaeus) and *Cucullia terensis* (Felder and Rogenhofer) (Lepidoptera: Noctuidae), which visited the flowers at dusk and early evening, confirming that the species is moth-pollinated.

Keywords: Moth pollination; Noctuidae; Petaloid scales; *Struthiola*; Thymelaeaceae

1. Introduction

The pollination biology of the southern African flora has been the subject of increasing interest over the past few decades (Johnson, 1994, 1997; Johnson and Liltveld, 1997; Johnson and Steiner, 2003; Donaldson et al., 2002; Manning and Snijman, 2002; Ollerton et al., 2003; Goldblatt et al., 1995; Johnson et al., 2005; and references therein), especially that of the Cape Region (Gemill et al., 2004). These studies, however, have focussed on relatively few families, primarily Geraniaceae (Struck, 1997), Iridaceae (Goldblatt and Manning, 2006) and Orchidaceae (Kurzweil and Weber, 1992; Johnson and Liltveld, 1997; Johnson et al., 2005). Our knowledge of the pollination ecology of most of the plant families in the southern African flora has thus advanced little since the pioneering observations of the last century by Marloth (1908) and Vogel (1954).

Most members of the Thymelaeaceae in southern Africa are assumed to be entomophilous (Vogel, 1954; Whitehead et al., 1987), with the exception of *Passerina*, which is known to be anemophilous (Bredenkamp and van Wyk, 1996). Some observations on the reproductive biology (but not pollination) have been made in the genus *Gnidia* (Beaumont and Edwards, in press) but nothing has been published on the pollination biology or pollinators of any of the apparently entomophilous genera of Thymelaeaceae. The genera *Gnidia* and *Struthiola* have been assumed to be pollinated by various Lepidoptera, both butterflies and settling moths (Vogel, 1954; Whitehead et al., 1987; Johnson, 1992).

Various authors have recorded the production of fragrance in the evening in *Struthiola* species (Marloth, 1925), raising the probability that the flowers are adapted for moth pollination. Indeed, the vernacular Afrikaans name for several species, *juf-fertjie-roer-by-die-nag* (the lady passes by in the night) (Smith, 1966), is a picturesque allusion to the attractive floral fragrance emitted in the evening. Apart from their nocturnal fragrance, the

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flowers of *Struthiola* display other features associated with phalaenophily, or pollination by settling moths (Faegri and van der Pijl, 1979), including a pale perianth, slender floral tube and included anthers.

The genus *Struthiola*, with some 40 species, is distributed throughout southern and tropical Africa, with a concentration of species in the fynbos vegetation in the southwestern Cape, where 21 species are recorded (Goldblatt and Manning, 2000). The species are typically ericoid shrublets, with spike-like inflorescences of narrowly tubular, white or cream-coloured flowers sometimes flushed with pink. The flowers are hypocrateriform and 4-merous, with a narrowly cylindrical tube, 4 subsessile stamens included within the tube and a whorl of 4–12 small, fleshy petaloid scales in the mouth of the tube.

The observations on moth pollination in *Struthiola ciliata* presented here are the first to be published on the pollination biology in the genus and on the role of the petaloid scales in the flower. The flowers of most species of *Struthiola* are remarkably similar in appearance, differing primarily in the length and vestiture of the hypanthium tube and in the number of petaloid scales, and the differences between the species are primarily vegetative (Wright, 1925). This suggests that species with a similar floral morphology to *S. ciliata* are also adapted to phalaenophily and that moth pollination is probably the most common strategy in the genus. Although reported in a few species of geophytes in the Cape flora (Johnson, 1997), moth pollination among fynbos shrubs has not been studied until now (Johnson, 1992). Our observations are thus also the first documented record of moth pollination in a fynbos shrub.

2. Materials and methods

2.1. Study sites

All observations were made during the late spring, in October and November 2005. Three populations were studied, one each at Kirstenbosch National Botanical Garden in Cape Town (33°59′S, 18°25′E), Mamre Wildflower Reserve (33°30′S, 18°25′E) and Blaauwberg Conservation Area (33°46′S, 18°29′E). Floral measurements were made on the Mamre and Kirstenbosch populations, fragrance analysis was done on the Mamre population, and pollinator observations were made on the Blaauwberg population. Voucher specimens (*Manning 2985*) of the Blauuwberg population are deposited at the Compton Herbarium (NBG).

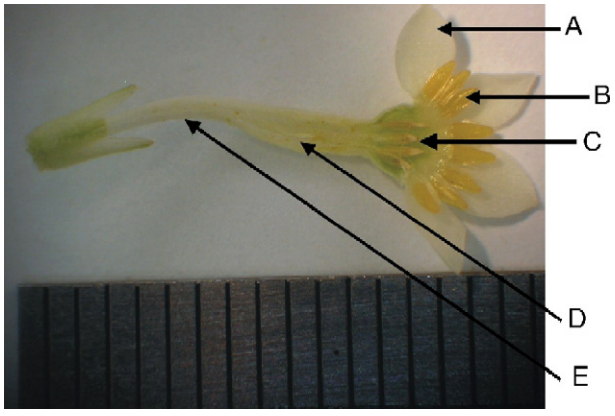

Fig. 1. Flower morphology in *Struthiola ciliata*. A = Sepals, B = Petaloid scales, C = Stamens, D = Style and E = Perianth tube.

Fig. 2. Petaloid scales and associated hairs, and pollen grains in anthers of *Struthiola ciliata*.

2.2. Pollinator observations

Plants were observed for floral visitors throughout the day and for several hours after sunset. Observations were terminated after it had been determined that moths were the only floral visitors. Floral visitors were collected for identification and voucher specimens were deposited at the South African Museum.

2.3. Fragrance analysis

Flowering branches were cut from the plants 2 h after sunset, at around 20h00, by which time the floral odour had fully developed. Several branches were retained in the dark and placed in water and the inflorescences enclosed within glass containers to concentrate the fragrance. Floral emissions were sampled throughout the night onto capillary tubes packed with Poropak by drawing air through the tubes with a vacuum pump (Manning and Snijman, 2002). Floral fragrance was analysed by R. Kaiser, Givaudan Schweiz AG, Fragrance Research, 8600 Dubendorf, Switzerland, by combined application of gas chromatography and mass spectrometry using a DB-Wax Capillary column (Kaiser, 1993).

Table 1
Distance between anthers and stigmas in flowers of different ages in *Struthiola ciliata*

Flower age	Anther-stigma distance (mm)
1 day	0.8–2.8 (1.48±0.83 S.D., n=5)
2 days	1.8–3.6 (n=2)
3 days	0.8–2.0 (1.35±0.99 S.D., n=4)
4 days	0.2–2.0 (1.33±0.99, n=3)
5 days	1.2 (n=1)

In order to locate the source of the floral fragrance on the flower, petaloid scales from approximately 20 flowers that were producing odour were excised and placed in a glass vial. The remaining portions of the flowers were placed in a second glass vial as a control and the contents of both vials were smelled after 30 min.

2.4. Nectar measurements

Nectar volumes and concentrations were measured in the morning from flowers of unknown ages picked from cut stems that had been collected the previous evening and placed directly in water and retained under ambient light conditions. Nectar volumes were determined individually but nectar concentrations were pooled from several flowers on account of the small volumes produced. The top of the floral tube was sliced off a short distance below the mouth and nectar was withdrawn by inserting a 2 μl capillary tube down to the base of the tube. The percentage of sucrose equivalents in fresh nectar was measured using a Bellingham and Stanley hand-held refractometer (0–50%).

Nectar production over time was investigated in both cut stems and in cultivated plants contained in greenhouses at Kirstenbosch. Flowers were labelled as they opened and those of different ages were sampled for nectar.

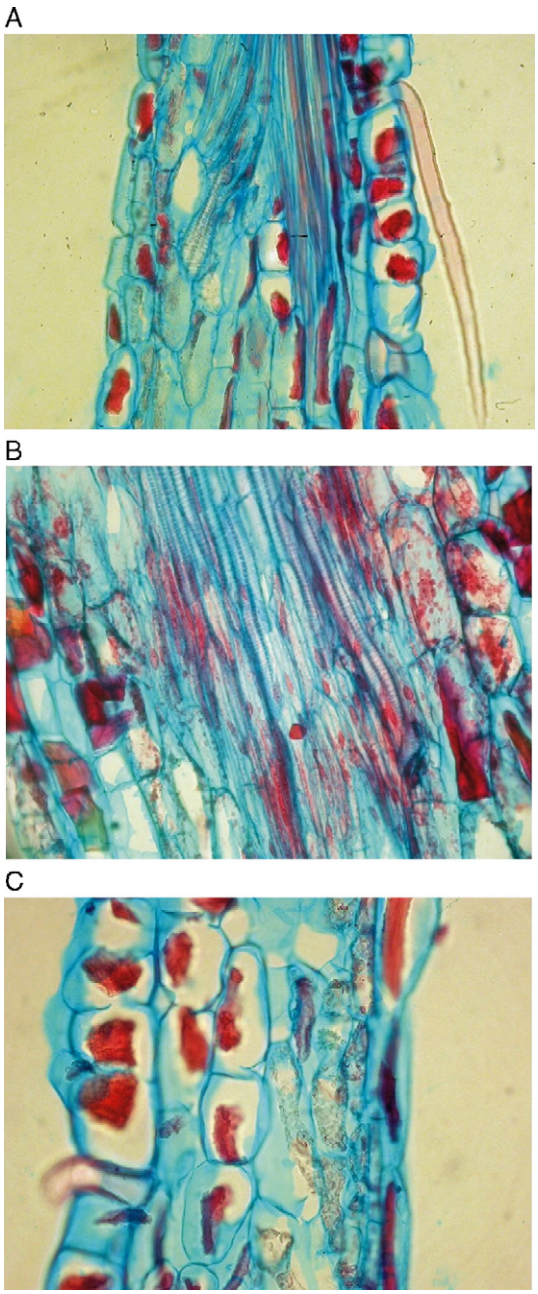

Fig. 3. Floral anatomy of *Struthiola ciliata*. The sepal mesophyll is parenchymatous and highly vacuolated (A), whereas the mesophyll of the petaloid scales is densely cytoplasmic, with a well-developed vascular bundle (B). Amyloplasts and idioblasts are restricted to the mesophyll of the upper part of the perianth tube (C).

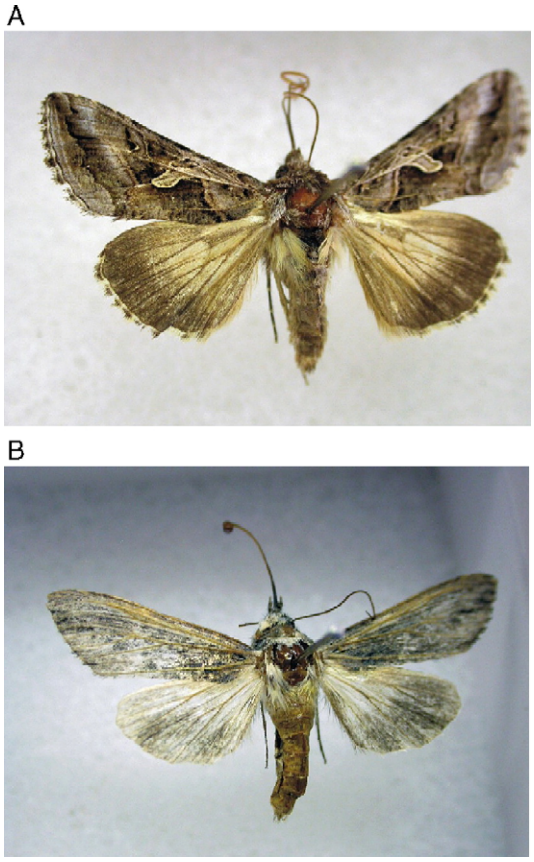

Fig. 4. *Syngrapha circumflexa* (A) and *Cucullia terensis* (B) (Lepidoptera: Noctuidae) collected visiting flowers of *Struthiola ciliata*.

2.5. Floral measurements

The lengths of the floral tube and style and the distances between the anthers and stigma were measured in 17 freshly picked flowers from the population at Mamre. The Kirstenbosch population was used to measure the distances between anthers and stigma in flowers of different ages.

2.6. Anatomical investigations

Fresh flowers were fixed in FAA, embedded in paraplast, sectioned at 12 μm using a rotary microtome, and stained with

alcian blue and safranin according to established methods (Rudall, 1995).

Pollen grains from fresh flowers were mounted directly on glass slides in Calberla's fluid (Ogden et al., 1974).

3. Results

3.1. Flower morphology and phenology

The flowers of *S. ciliata* are hypocrateriform and creamy white in colour, with a slender floral tube 18–24×2–3 mm in diameter. The sepals are elliptical and 3–4 mm long. Eight fleshy, ellipsoidal, hairy petaloid scales 0.6–0.9 mm long surround the mouth of the tube (Figs. 1 and 2). Four subsessile stamens are included within the tube just below the mouth. Anthesis occurs in the evening at ±18h00, at which time the sepals open and the anthers dehisce. The perianth shows no further movements during the life of the flower. It was not ascertained at what stage the stigma becomes receptive.

Anthesis is synchronised on individual plants so that several flowers open each evening. Individual flowers last for 9–11 days, and each plant is in flower for up to 2 weeks. Nectar accumulates in the lower part of the hypantium during the first 3 to 4 days but diminishes from the fifth day onwards and is presumably reabsorbed. Flowers are unscented during the day but emit a strong fragrance at dusk and continue to do so throughout the night. The production of fragrance ceases in the early morning. Fragrance production continues nightly throughout the life of the flower.

Style length ranges from 16 to 19 mm (17.59±0.78 S.D., $n=17$) and the distance between anthers and stigma is 0.0–7.5 mm (4.07±1.99 S.D., $n=17$). In most flowers, the stigma is located below the anthers (Table 1, Fig. 1) and only rarely at the same level as the anthers. The variation in the distance between anthers and stigmas in flowers on the same plant did not correlate with the age of the flowers (Table 1).

Anatomically, the sepals comprise a 4-seriate, highly vacuolate, parenchymatous mesophyll, with tanniniferous inclusions in the epidermal cells on both surfaces (Fig. 3A). The epidermal cells of the petaloid scales are similarly tanniniferous but the mesophyll is densely cytoplasmic and contains numerous lipid droplets (Fig. 3B). A well-developed central vascular bundle passes into each of the petaloid scales. Cells of the inner layers of mesophyll in the upper part of the hypanthium tube are densely packed with amyloplasts and are interspersed with scattered idioblasts containing solitary large druses (Fig. 3C).

3.2. Pollinator observations

The only floral visitors observed were the moths *Cucullia terensis* (Felder and Rogenhofer, 1874) (Fig. 3) and *Syngrapha circumflexa* (Linnaeus, 1767) (Fig. 4) (Lepidoptera: Noctuidae), which visited the flowers at dusk and early evening. During the period 18h30–19h30 at least 10 visits to the plants under observation were seen, after which observations were suspended. Moths probed several flowers in each inflorescence in succession before moving to another inflorescence, either on the same plant or on nearby plants. Visits to individual flowers were brief, lasting just a few seconds each. During each visit, the moth either settled on the flower while continuing to vibrate its wings, or merely clasped the sepals with its legs while continuing to hover.

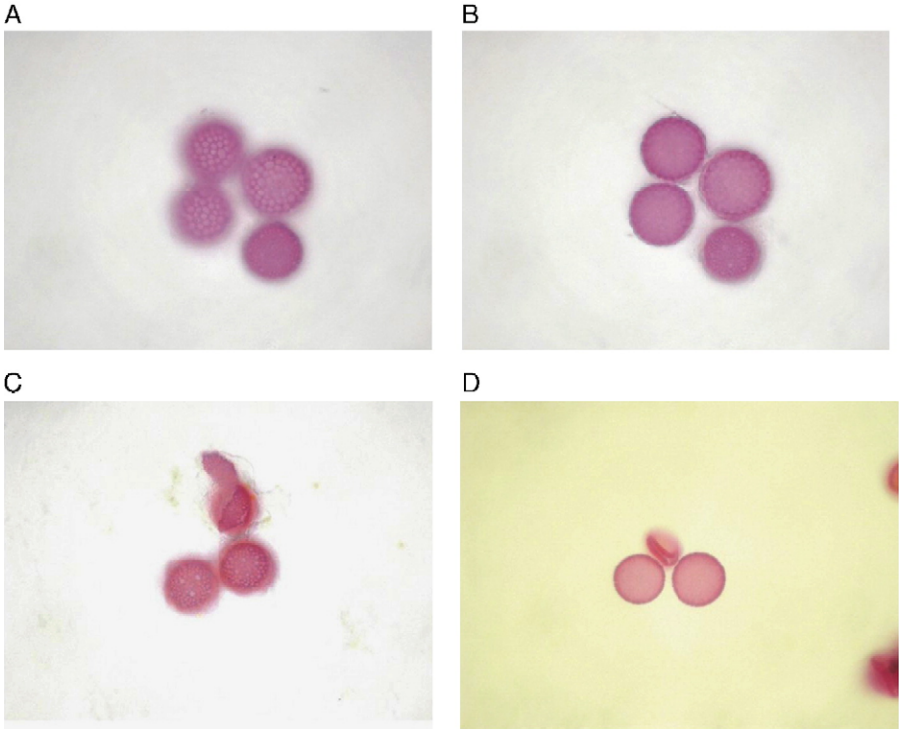

Fig. 5. Pollen grains collected from the moth proboscides (A and B) and pollen grains of *Struthiola ciliata* (C and D).

Table 2
Chemical composition of floral scent in *Struthiola ciliata* from Mamre Wildflower Reserve (*italicised* compounds represent principal compounds detectable to the human nose)

Compound	Percentage
Fatty acid derivatives	
Alkanes	
A 5 (or 6)-Tridecene	7.30
A Pentadecene	1.10
Pentadecane	0.20
Tridecane	5.60
Undecane	1.50
Subtotal	15.7
Esters	
(*Z*)-3-Hexenyl acetate	0.10
(*Z*)-5-Tetradecenyl acetate	0.50
Dodecyl acetate	1.30
Hexyl acetate	0.02
Methyl laurate	0.02
Methyl myristate	0.40
Methyl palmitate	0.04
Methyl palmitoleate	1.20
Octyl acetate	0.02
Tetradecyl acetate	0.20
Subtotal	3.8
Benzenoids	
3-Phenylpropyl acetate	0.10
Benzaldehyde	0.20
Benzyl acetate	10.30
Benzyl alcohol	0.40
Benzyl isobutyrate	0.05
Cinnamic alcohol	0.02
Cinnamyl acetate	0.10
Eugenol	0.20
Vanilline	0.02
Subtotal	11.39
Isoprenoids	
Monoterpenes	
(*E*)-3(4)-Epoxy-3,7-dimethyl-1,6-octadiene	1.30
(*E*)-Ocimene epoxide	1.70
(*E*,*E*)-2,6-Dimethyl-3,5,7-octatrien-2-ol	0.10
(*Z*)-3(4)-Epoxy-3,7-dimethyl-1,6-octadiene	0.20
(*Z*)-Ocimene epoxide	0.20
(*Z*)-Ocimene	1.20
3,7-Dimethyl-1,6-octadien-3,4-diol	0.20
6-Methyl-5-hepten-2-yl acetate	0.04
Carvone hydrate	0.07
cis-Limonene epoxide	0.08
cis-Sabinene hydrate	1.10
cis-Verbenol	0.06
(*E*)-Ocimene	11.00
Eucalyptol	1.70
Geraniol	0.40
Geranyl acetate	0.40
Ipsdienol	0.20
Ipsdienyl acetate	0.30
Isopinocamphone	0.10
Isothujone	0.30
Limonene	0.50
Linalool	1.60
Myrcene epoxide	0.10
Myrcene	1.60
Myrtanol	0.02
Myrtenol	0.10
Nerol	0.20
p-Cymen-8-ol	0.03
Isoprenoids	0.20
Monoterpenes	
Rose furan	
Sabinene	2.00
Terpinen-4-ol	0.60
Terpinolene	0.03
Thujone	0.05
trans-Carveol	0.03
trans-Limonene epoxide	0.03
trans-Pinocarveol	0.60
trans-Sabinene hydrate	2.20
trans-Sabinol	0.30
trans-Verbenol	1.20
trans-Verbenone epoxide	0.70
Verbenone	5.00
p-Cymene	0.60
α-Pinene	0.20
β-Pinene	1.00
γ-Terpinene	0.10
α-Terpineol epoxide	0.20
α-*Terpineol*	18.00
Subtotal	57.84
Sesquiterpenes	
(*E*,*E*)-4,8,12-Trimethyl-1,3,7,11-tridecatetraene	0.80
(*E*,*E*)-Farnesyl acetate	0.10
Bicyclogermacrene	0.20
Germacrene A	0.04
Methyl (*E*,*E*)-3,7,11-trimethyl-2,6,10-dodecatrienoate	1.70
Nerolidol	0.70
Prezizaene	0.30
trans-α-Bergamotene	0.60
Zizaene	0.30
Subtotal	4.74
Other	
(*E*)-2-Methylbutyraldoxime-*O*-methyl ether	0.02
Subtotal	0.02
Total	93.53

Pollen grains collected from the proboscides of both moth species (Fig. 5A and B) matched those of *S. ciliata* (Fig. 5C and D) and were assumed to be from that species. The proboscis in specimens of both species was 17–19 mm long and pollen grains were found along most of the length, from the tip to 4–6 mm from the base.

3.3. Fragrance analysis

The floral fragrance of *S ciliata* is sweet, spicy and somewhat coniferous to the human nose, and contains several classes of compounds, including alkanes, esters, benzenoids, monoterpenes and sesquiterpenes (Table 2). Monoterpenes account for 57.8%, alkanes 15.7%, esters derived from fatty acids for 3.8%, benzenoids for 11.39% and sesquiterpenes for 4.74% of the total. Individual compounds range in relative concentration from 0.02% to 18.00%. Chemically, the fragrance is dominated by α-terpineol (18%), benzyl acetate (10%) and A 5 (or 6)-tridecene (7.3%), with smaller amounts of dodecyl acetate (1.3%) and methyl (*E*,*E*)-3,7,11-trimethyl-2,6,10-dodecatrienoate (1.7%). The most significant compounds detectable by the

human nose are thujone, isothujone, verbenone, α-terpineol, benzyl acetate, eugenol and vanilline (R. Kaiser, pers. com.).

3.4. Nectar

Fresh flowers contain small volumes, 0.025–0.188 μl (0.10 ± 0.07 S.D., $n = 10$) of relatively dilute nectar (20–34% sucrose equivalents).

4. Discussion and conclusion

S. ciliata displays the floral features typically associated with pollination by settling moths (Van der Pijl and Dodson, 1966). The perianth is pale-coloured, with a long, slender floral tube and included anthers. Fresh floral buds open in the evening and flowers emit a sweet, spicy floral odour only at night. The relatively dilute nectar that is produced is also typical of moth-pollinated species (Baker and Baker, 1982). *S. ciliata* is visited by at least two species of noctuid moths, but it is possible that further investigation across the range of the species may implicate further moth species in its pollination.

The floral fragrance in *S. ciliata* is produced by the petaloid scales alone. The well-vascularised, densely cytoplasmic nature of the petaloid scales is visible evidence of their role as metabolically active osmophores, and the presence of numerous lipid droplets is consistent with the predominance (±58%) of isoprenoid compounds in the fragrance profile. The large reserves of amyloplasts in the tissue of the floral tube are probably the source of the metabolic energy required for the synthesis and release of the floral fragrance. Starch-rich tissue implicated in scent emission has also been identified in several orchids, with the amyloplasts either within the cells of the osmophore itself (Stern et al., 1987) or in subadjacent tissue (Vogel, 1962; Pridgeon and Stern, 1983). The location of the starch-rich tissue in the floral tube of *S. ciliata* at some distance from the osmophores on the petaloid scales is thus unusual.

The identification of the role of the petaloid scales in *S. ciliata* as osmophores represents a significant advance in our understanding of their significance in the genus, and suggests a possible adaptive significance for the variation in size and number of the scales in different species of *Struthiola*. The homology of the petaloid scales in Thymelaeaceae has long been unclear and they are still regarded as homologous with petals by some authors (Hilliard, 1993). As a result of anatomical investigations, however, it seems that they are most likely to be stipular appendages of the sepals (Heinig, 1951). If this interpretation is correct, then the basic number of scales per flower is eight (two per sepal). The increase in scale number to 12 that is evident in several species from the southwestern Cape (Goldblatt and Manning, 2000) may thus represent a strategy for increasing the area of scent production but this remains to be investigated. The presence or absence of scent in species with highly reduced scales, such as *S. anomala* (Hilliard, 1993) is also unknown.

The cessation of nectar production mid-way through the life of the flowers, unlike fragrance production which continues for the life of the flower, is most obviously interpreted as a method of conserving energy, although there is evidence that the fynbos flora is not carbohydrate-limited (Stock and Allsopp, 1992). An alternative interpretation is that it is a mechanism for reducing the time spent by the pollinator in visiting older flowers that are more likely to have been pollinated by removing the reward. This is achieved without reducing the 'floral silhouette' of the plant since each flower continues to produce scent even after nectar production has ceased. Alternatively, reducing the time spent visiting older flowers may be a way of maximising the rate at which pollen transfer takes place in older flowers. The fact that each flower contains a single ovule means that very few, theoretically just one, pollen grain is required per stigma for complete seed-set. The relative balance of male and female fitness in Thymelaeaceae deserves further study.

Floral variation between the species of *Struthiola* is modest (Wright, 1925), extending primarily to differences in the number of the floral scales and to some variation in the length of the floral tube. In addition, the nocturnal production of floral fragrance is characteristic of other species, including *Struthiola leptantha* Bolus and *Struthiola tomentosa* Andrews (unpublished observations). It is thus probable that moth pollination is widespread in the genus. No species, however, produces flowers with a tube longer than 30 mm, which appears to be the lower limit of sphingophily (Manning and Snijman, 2002) in the southern African flora. Species of the related genus *Gnidia* with similar flowers are also likely to be phalaenophilous, but floral variation in that genus is much greater, indicating a correspondingly greater variety of pollination systems. Nevertheless, some 60 species of these two genera in the Cape Region have flowers that conform to the syndrome of phalaenophily as observed in *S. ciliata* (Goldblatt and Manning, 2000), suggesting that this pollination system is important in the Cape flora.

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